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Evaluation of Minnesota Geographic Classifications Based on Caddisfly (Trichoptera) Data

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ABSTRACT

The ability to partition the variation of faunal assemblages into homogenous units valuable for biomonitoring is referred to as classification strength (CS). In this study, the CSs of three types of geographic classifications: watershed basin, ecological region, and caddisfly region, were compared based on 248 light trap samples of adult caddisflies collected in Minnesota during 1999–2001. The effect on CS of three different levels of taxonomic resolution: family, genus, and species, was also assessed. Primary (broadest possible) *a priori* classification by watershed basin and ecological region had a lower CS than did secondary classification by these regions. Caddisfly region, an *a posteriori* classification based directly on caddisfly distribution data, had nearly twice the CS of any *a priori* classification. CS decreased approximately 20% with a decrease in taxonomic resolution from species to genus, and from genus to family. These results suggest that geographic classification, spatial scale, and taxonomic resolution are all important factors to consider when sampling aquatic insects, and that widely used *a priori* geographic classifications are not the ideal units for sampling the aquatic biota.

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A premise underlying *a priori* geographic classifications, such as watershed basin, is that sites within each determined class are similar to each other in their physical and biological properties; natural variation within classes should be lower than variation among classes (Omernik 1987, Omernik and Griffith 1991). If effective, such classifications become important organizational tools for predicting biological variation between ecosystems. The premise of site similarity within site classes is important for biomonitoring because it implies that biological responses to human disturbance of a site can be measured by comparing the organismal assemblages of a disturbed site to those of determined reference sites within the same class (Hughes and Larsen 1988, Hughes 1989, Omernik and Bailey 1997). Being able to predict assemblages based on class is the foundation of common empirical bioassessment models such as RIVPACS, AusRivAs, and BEAST (e.g., Norris 1995). An appropriate classification should, therefore, minimize natural variation among reference sites within each class, and partition the variation within a fauna into homogenous regions (Hughes and Larsen 1988, Hughes 1989).

Two of the most commonly used *a priori* geographic classifications pertaining to aquatic biomonitoring are ecological region (e.g., Coniferous Forest) and watershed basin. The former is based on factors such as geology, vegetative cover, and climate, whereas the latter consists of all of the geographic area that drains into a common outlet (Bailey 1980, Omernik 1987). Both of these classifications can be applied at different spatial scales. Primary or first-level watershed basins (e.g., the Mississippi River) drain directly into the ocean and are the largest determinable hydrologic units. Secondary and succeeding-level watersheds are then subsets of the broader watershed classes draining into a common outlet. Primary ecological regions, often termed biotic provinces or biomes, are the broadest ecological classifications possible, with succeeding levels nested within them (Bailey 1980).

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Since neither watershed basin nor ecological region is created using aquatic organismal distribution data, neither may optimally partition the variation of organismal assemblages (Sokal 1974). It becomes important, therefore, to test the relative strength of these classifications in providing such separation before using them as units to sample aquatic biota. Otherwise, comparisons between disturbed and reference sites within classes will be of diminished value (Hughes and Larsen 1988, Hughes 1989, Omernik and Bailey 1997). The ability of a classification scheme to partition the variation in faunal assemblages into homogenous units is referred to as its classification strength (CS) (Van Sickle 1997).

Hawkins et al. (2000) reviewed the literature on CS, summarizing both aquatic vertebrate and invertebrate studies. They found that watersheds and ecological regions typically had similar CSs. Both classification schemes applied at secondary or succeeding levels tended to have higher CS than did those applied at primary levels. Regions created from distribution data of studied organisms, termed *a posteriori* classifications, almost always had higher CS than did *a priori* regions. Increasing the level of taxonomic resolution from family to genus or species almost always increased CS, regardless of the classification scheme used.

The state of Minnesota is situated at the intersection of the three largest biotic provinces of North America: Coniferous Forest, Deciduous Forest, and Prairie (Fig. 1) (Bailey 1980). These three provinces are subdivided into 10 ecological sections (secondary ecological regions) (Hanson and Hargrove 1996). Minnesota is likewise uniquely located at the intersection of three primary watersheds: Hudson Bay, Mississippi River, and Saint Lawrence Seaway (Fig. 1), which are divided into eight secondary and 81 tertiary watersheds, often termed watershed provinces and major watersheds, respectively (Schwartz and Thiel 1954, USGS 2002). Several environmental variables, including climate, geology, soil type, vegetative cover, topographic relief, and level of human disturbance vary notably from north to south or east to west within Minnesota (Borchert and Yaeger 1968, Wright 1972, Anderson and Grigal 1984, Baker et al. 1985, Coffin 1988, Tester 1995). The ecological and aquatic diversity of the state, therefore, provides several different criteria for classification, as well as an ideal location for evaluating CS. Furthermore, due to ecological affinities between Minnesota and adjacent states and provinces, evaluation of the biota may have a broad regional application (Bailey 1980, Tester 1995).

The caddisflies (Trichoptera) are an important group for biomonitoring due to their high species richness, ecological diversity, varying susceptibilities to different types of human disturbance, and abundance in virtually all types of freshwater ecosystems (Mackay and Wiggins 1979, Rosenberg and Resh 1993, Merritt and Cummins 1996, Barbour et al. 1999, Dohet 2002). For biomonitoring purposes it is, therefore, important to find a classification scheme that successfully partitions natural variation of the Minnesota caddisflies into homogenous regions. A classification that does so will have a have high caddisfly CS and will be an appropriate unit for caddisfly sampling.

Using detrended correspondence analysis (DCA) and a flexible unweighted pair-group method using arithmetic averages (UPGMA) algorithm, Houghton (2004) grouped 58 Minnesota secondary watersheds into five regions of caddisfly biodiversity based on caddisfly relative abundance data (Fig. 2). As an *a posteriori* classification created using caddisfly data, caddisfly region was assumed to be the optimal partitioning of faunal variation within Minnesota. It should, therefore, have a higher CS than *a priori* classifications that ignore caddisfly distribution data.

In this study, despite some difference in mean unit size, caddisfly region (mean size = 28,818 km^2), primary watershed (mean = 48,031 km^2), and biotic province (mean = 48,031 km^2) were considered to be on a similar spatial scale since all three represented the broadest determinable units within the respective classification
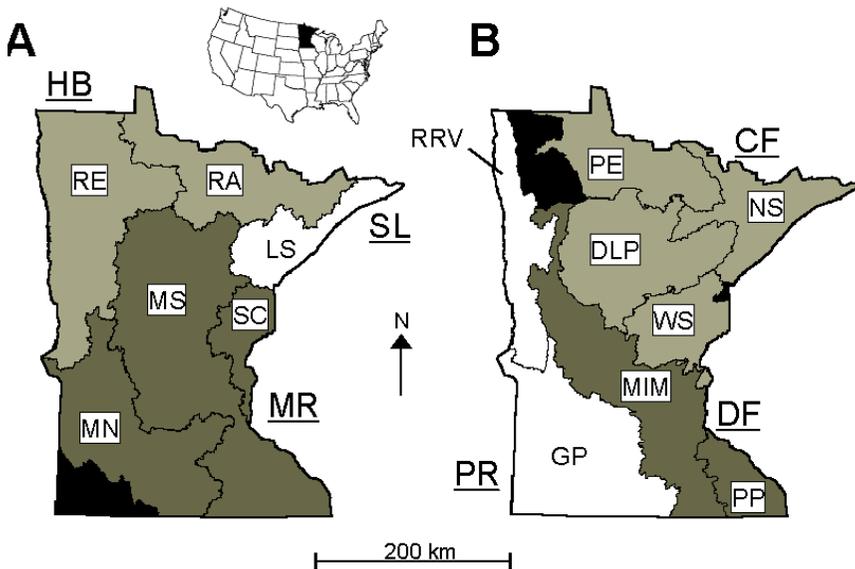
Figure 1. Location of Minnesota showing two geographic classifications. A. Primary watersheds (underlined), HB = Hudson Bay, MR = Mississippi River, SL = Saint Lawrence Seaway, divided into secondary watersheds (regular type), LS = Lake Superior, MN = Minnesota River, MS = Mississippi River, RA = Rainy River, RE = Red Rver, SC = Saint Croix River (USGS 2002). B. Biotic provinces (underlined), CF = Coniferous Forest, DF = Deciduous Forest, PR = Prairie, divided into ecological sections (regular type), DLP = Drift and Lake Plains, GP = Glaciated Plains, MIM = Minnesota and Iowa Morainal, NS = Northern Superior Uplands, PE = Peatlands, PP = Paleozoic Plateau, RRV = Red River Valley, WS = Western Superior Uplands (Bailey 1980, Hanson and Hargrove 1996). Darkened areas correspond to areas that had insufficient sample size to be included in any analysis.

Figure 2. The five caddisfly regions of Minnesota determined by grouping together Minnesota's 81 major watersheds (Houghton 2004) and the 248 sampling sites of this study. Overlap occurs between sample markers. Regions: LS = Lake Superior, NO = Northern, NW = Northwestern, SE = Southeastern, SO = Southern.
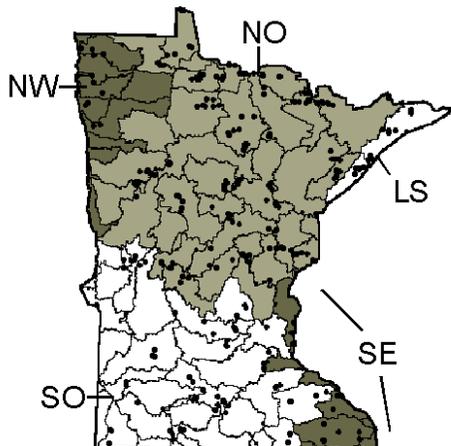
regimes. Secondary watershed (mean = 24,015 km²) and ecological section (mean = 18,011 km²) were also considered to be on a similar spatial scale.

This study had three main objectives. The first was to compare the CSs of caddisfly region, ecological region, and watershed basin based on caddisfly data. This comparison will determine if the created caddisfly regions have a greater value as caddisfly sampling units than alternative *a priori* classifications. The second objective was to compare the CSs of first and second-level watershed and ecological region classifications to assess the effects of spatial scale. The third objective was to assess the effects of three levels of taxonomic resolution—family, genus, and species—on CS of all classifications.

MATERIALS AND METHODS

Sampling. Adult caddisflies were sampled during June and July, the peak period of emergence and flight activity in Minnesota (Monson 1996, Houghton 2004). All collecting sites were visited once. Between three and 12 samples were collected from 58 of Minnesota's 81 major watersheds yielding a broad distribution of sampling sites (Fig. 2).

The goal of sampling was to maximize the amount of diversity captured within a region so that CS of entire regions could be compared. To that effect sampling sites were divided into six site classes (Table 1); five of these classes were based on stream width estimated at the sampling site; the sixth class constituted lakes and wetlands. Stream classes were constructed based on the approximate stream width divisions of the River Continuum Concept (RCC), thereby inferring ecological information about each habitat (Vannote et al. 1980). At least four samples were collected from most of the 58 major watersheds completely within Minnesota (Fig. 1), representing one small stream (Class 1–2), one medium stream (3), one large river (4–5), and one lake or wetland (Table 1), thus sampling the major habitat types representatively. Sampling sites were found using DeLorme (1994), and were estimated to be the least disturbed of their respective watersheds based on observed upstream land use. Most were located in officially protected areas such as State Parks and Forests.

Caddisflies were sampled at each site with an ultraviolet light trap, which consisted of an 8-watt portable ultraviolet light placed over a white pan filled with 70% EtOH. These traps were placed adjacent to aquatic habitats at dusk and retrieved approximately two hours after dusk. While not an exhaustive technique—a few caddisfly species are day-flying or not attracted to lights—standardizing the time of collection, weather conditions, wattage of the light source, and size of collecting pan likely yielded a representative sample of the nocturnally active caddisfly adults and allowed for comparisons among sites (Myers and Resh 1999, Nakano and Tanida 1999). Several studies have suggested that most adult caddisflies disperse <100 m from the natal habitat (Nielsen 1942, Svensson 1974, Göthberg 1973, Sode and Wiberg-Larson 1993, Peterson et al. 1999, Sommerhäuser et al. 1999). Since virtually all of the sampling sites in this study were separated by >5000 m, dispersal of adults among sites was assumed to be negligible. To standardize weather conditions, samples were taken only on days with peak daytime temperature >22°C, dusk temperature >13°C, and without precipitation or noticeable wind at dusk (Resh et al. 1975; Anderson 1978; Waringer 1989, 1991; Anderson and Vondracek 1999, Houghton 2004). Larvae were not collected as most are not identifiable to the species level and species-level identification was necessary for this study.

All specimens were identified to the species level except for some females of the widely distributed families Hydropsychidae, Hydroptilidae, and Polycentropodidae, which lack characters necessary for species-level female identification. Such specimens were not included in any analysis. All identified specimens were counted and entered into the relational database Biota (Colwell

Table 1. The six site classes constructed for this study and the total number of samples taken from each. Stream width was estimated at each sampling site.

Class	Description	Width	Sample Size
1.	Small Stream	<2m	24
2.	Small/medium Stream	2-4m	37
3.	Medium River	4-10m	71
4.	Medium/large River	10-30m	54
5.	Large River	>30m	20
L.	Lake or Wetland	N/A	42

1996). All specimens collected during this study were deposited in the University of Minnesota Insect Museum (UMSP).

Analysis. Sorensen coefficients (Sorensen 1948) were calculated for all pair wise combinations of samples using caddisfly species presence/absence data. The Sorensen coefficient is a commonly used expression of the similarity of taxa between sites, and ranges from 0 (no species in common) to 1 (all species in common). Classification strength was calculated as $CS = W - B$, where W was the mean of all individuals within-class site similarities (W_i) weighted by sample size, and B is the mean of all between-class site similarities (Smith et al. 1990, Van Sickle 1997). A value of W that was large relative to the value of B meant that the classes contained sites that were more similar to each other than they were to sites in other classes (Van Sickle 1997, Van Sickle and Hughes 2000). Thus, classes successfully partitioned natural variation into homogenous units and, consequently, had a high CS. Calculations of W_i and W were made for each classification using the MRPP function of the program PC-ORD for Windows® (Mielke et al. 1976, McCune and Medford 1997). Calculations of B and overall CS for each classification were made using the freeware program MEANSIM6 for Windows® (http://www.epa.gov/wed/pages/models/dendro/mean_similarity_analysis.htm), which uses output from the MRPP function to make these calculations.

Values of W_i, W, B, and overall CS were determined for each classification scheme. These values were plotted as mean similarity dendrograms, with W_i - B for each individual class represented as individual branch lengths on a dendrogram. This representation allowed for graphic comparison of the relative CSs of the various classifications and classes. The value of each CS was tested for statistical significance against the null hypothesis of *no class structure* by using a permutation procedure (Mielke et al. 1976, Clarke and Green 1988, Smith et al. 1990). In this procedure, the determined CS of a chosen classification scheme was compared with a CS determined by a random grouping of the same sites. The probability value (*P*) of the test is estimated from the proportion of 10,000 randomly chosen groups having a larger CS than the tested classification (Jackson and Somers 1989, Van Sickle 1997).

RESULTS

A total of 306,541 caddisfly specimens were analyzed based on samples from 248 aquatic habitats within 58 Minnesota watersheds (Fig. 2). Twenty-one samples were collected in 1999, 169 in 2000, and 58 in 2001. There was no significant difference in either mean species richness ($P = 0.40$, $\delta = 7.17$) or mean specimen abundance ($P = 0.10$, $\delta = 119.1$) among samples of the three years of this study (One-way Analysis of Variance), suggesting that potential differences between years did not affect the study results.

CSs ranged from 2% to 17% and all tested groupings exhibited a statistically significant CS (Figs. 3–5). CS of caddisfly region was the highest (12–17%)

among classifications across the three taxonomic levels, exhibiting approximately twice the CS of any other classification at the same taxonomic scale (Figs. 3–5). All individual classes of caddisfly region had CS >5% at the species level.

At a similar spatial scale, ecological region had a higher CS than watershed at all taxonomic levels (Figs. 3–5). Biotic province had a higher CS than primary watershed, whereas ecological section had a higher CS than secondary watershed. Biotic province had approximately the same CS as secondary watershed (Figs. 3–5).

At all three levels of taxonomic resolution, secondary groupings of both watersheds and ecological regions had higher CSs than did primary groupings (Figs. 3–5). For both watersheds and ecological regions, values of B were similar for both primary and secondary groupings. Values of W_i were, in general, higher with secondary groupings (Figs. 3–5).

CS increased with increased taxonomic resolution for all classifications (Figs. 3–5). On average, CS decreased by approximately 0.02 between levels of resolution for all classifications. Individual classes of all classifications generally maintained their CS relative to other classes at the different levels of resolution (Figs. 3–5). Both B and W decreased as taxonomic resolution increased; however, W exhibited a smaller decrease than B (Figs. 3–5). Within caddisfly regions 12% of CS was lost when decreasing the taxonomic resolution from species (CS = 0.17) to genus (CS = 0.14), and another 20% was lost from genus to family (CS = 0.12) (Fig. 6). A similar trend emerged with both watersheds and ecological regions at both primary and secondary scales (Fig. 6).

DISCUSSION

Statistical and Biological Significance. All tested groupings exhibited a statistically significant CS (Figs. 3–5). Statistical significance, however, may have been misleading. Van Sickle and Hughes (2000) argued that permutation tests for CS are too powerful, especially with sample size >50, and that even weak CSs will likely be deemed significant. Sample size for this study was 248 sites. Because tests of CS are against a model of *no class structure*—a completely random grouping of sites—it is difficult to translate statistical significance into biological significance. A CS of 2% may be statistically significant, yet is only 2% better at partitioning faunal variation than is a random site grouping. For this reason several workers have suggested that the *no class structure* model is not particularly informative, and that considerably more information can be learned from comparing the biological "significance" (dendrogram branch lengths) of competing classifications rather than by testing the statistical significance of a single classification (Green 1980, Gordon 1981, Yocoz 1991, Stewart-Oaten et al. 1992, Hillborn and Mangel 1997, Van Sickle and Hughes 2000).

Caddisfly Regions. Caddisfly regions had approximately double the CS of other classifications at the same taxonomic resolution (Figs. 3–5). This result is not surprising. Caddisfly regions were created using caddisfly data specifically, as opposed to other physical or biological data. The classification should, therefore, have yielded a better partitioning of the fauna than *a priori* classifications. The lower CSs of the Lake Superior and Southeastern regions was due to consistently low values of W_i, perhaps caused by the topographical variation and subsequent heterogeneity of sampling sites of these regions. Houghton (2004) found that these two regions had a lower Morita-Horn index of biological similarity (Margurran 1988) than the other regions, reflecting their high site heterogeneity.

Since caddisfly regions were determined from collections made during 1999–2001, they reflect anthropogenic disturbance, whereas watersheds and ecological regions are based entirely on the best determination of natural conditions (Bailey 1980, USGS 2002). All samples in this study were taken from the
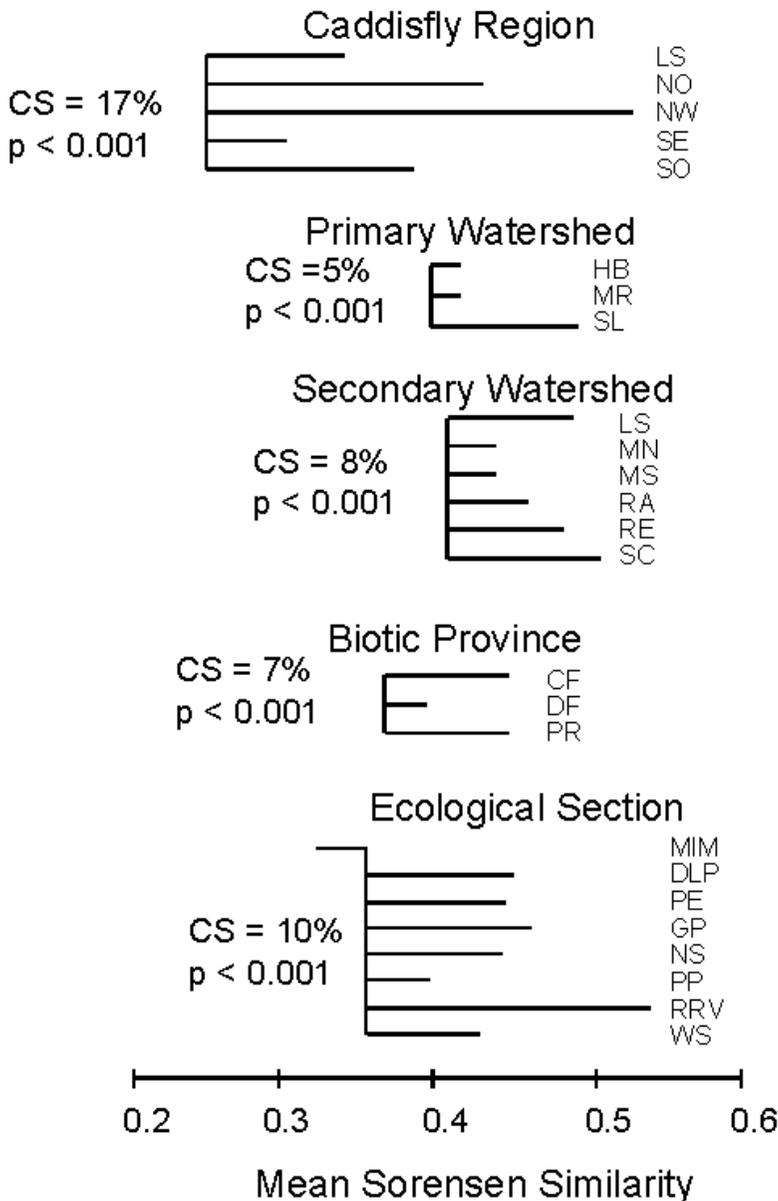
Caddisfly Region

CS = 17%
p < 0.001

LS
NO
NW
SE
SO

Primary Watershed

CS =5%
p < 0.001

HB
MR
SL

Secondary Watershed

CS = 8%
p < 0.001

LS
MN
MS
RA
RE
SC

Biotic Province

CS = 7%
p < 0.001

CF
DF
PR

Ecological Section

CS = 10%
p < 0.001

MIM
DLP
PE
GP
NS
PP
RRV
WS

0.2   0.3   0.4   0.5   0.6

Mean Sorensen Similarity

Figure 3. Mean similarity dendrograms for caddisfly region, watershed, and ecological regions using presence or absence of Minnesota caddisfly species. For each dendrogram, the node (vertical line) is plotted at the mean between-class similarity (B) for each grouping, and the end of each horizontal branch is plotted at the mean within-class similarity for the individual class (W_i). Classification Strength (CS) is the mean length of dendrogram branches for each class weighted by sample size, and is calculated with the formula CS = W - B.
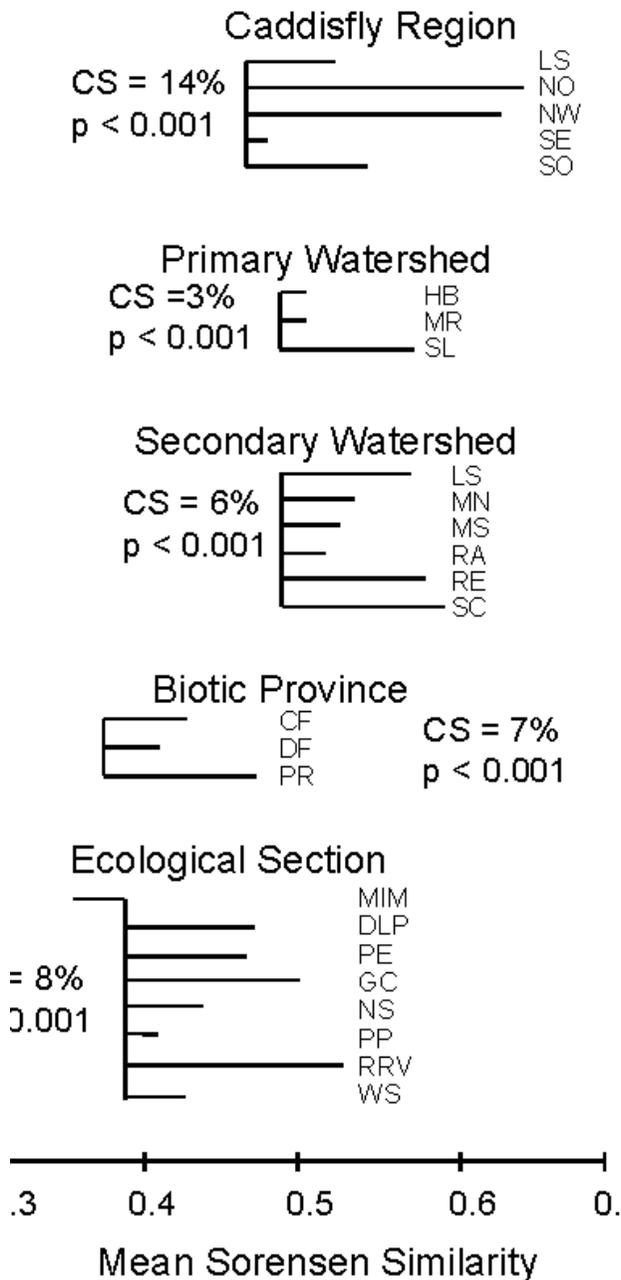
Figure 4. Mean similarity dendrograms for caddisfly region, watershed, and ecological regions using presence or absence of Minnesota caddisfly genera. See Figure 3 for further explanation.
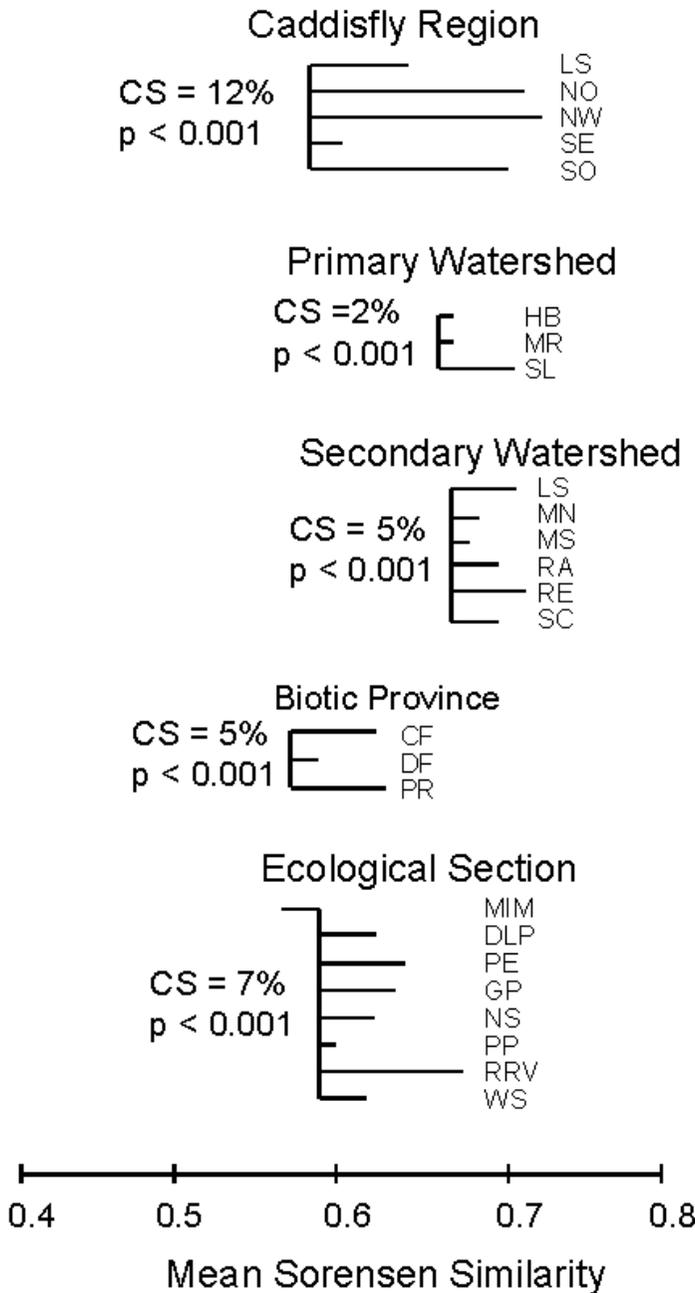
Figure 5. Mean similarity dendrograms for caddisfly region, watershed, and ecological regions using presence or absence of Minnesota caddisfly families. See Figure 3 for further explanation.
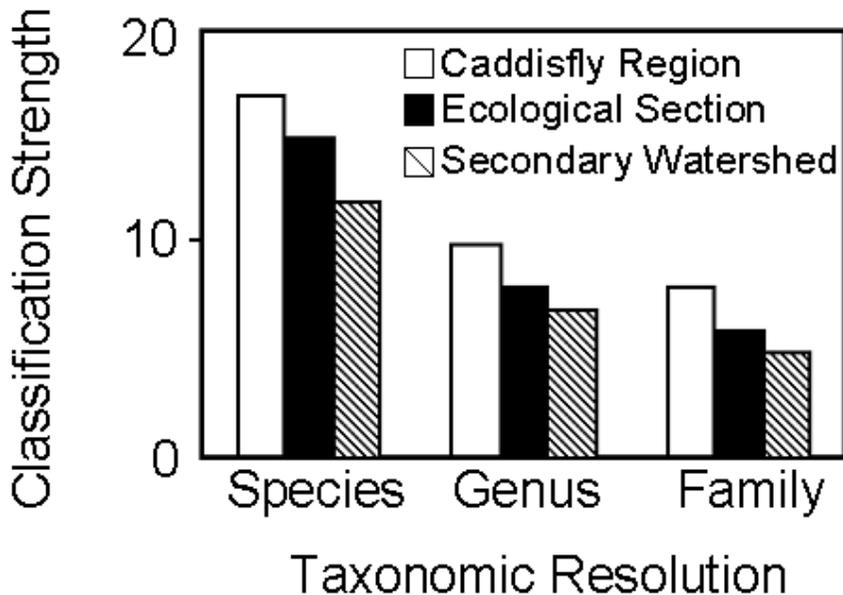
Figure 6. CS at three levels of taxonomic resolution for the three strongest geographic classifications, based on Minnesota caddisfly presence or absence.

perceived least disturbed habitats within the individual ecosystems. "Least disturbed", however, may be relative. Much of northeastern Minnesota remains forested while almost all of northwestern and southern Minnesota has been converted to agricultural or urban environments (USGS 1999). Sites truly undisturbed by human activity may not exist in these areas. Houghton (2004) found that the relative percentage of disturbed upstream habitat correlated with caddisfly species composition in Minnesota, likely contributing to the higher CS of caddisfly region.

Despite the perceived best possible partitioning of the caddisfly fauna by caddisfly region, these regions still had relatively weak (<20%) CSs. These values were consistent with those of previous studies; only rarely were CS values >20%, even for *a posteriori* classifications (see Hawkins et al. 2000). This low CS may leave the majority of faunal variation unaccounted for by even the best determined classifications. Individual species distributions are continuous, and forcing a discrete model on to a series of such continuous distributions is artificial (Hawkins and Vinson 2000). Wide-ranging species that occur in more than one class raise the value of B, which lowers overall CS. Secondly, within-class environmental heterogeneity—whether caused by natural or anthropogenic factors—lowers the value of W, which also lowers CS. Some of this heterogeneity may have been mitigated because caddisfly regions incorporated anthropogenic factors. Watersheds and ecological regions likely had lower CSs because they did not incorporate such factors.

All classifications may simply have been too coarse to successfully partition the caddisfly fauna. A substantial amount of within-class heterogeneity was likely added to all classifications including caddisfly regions by intentionally sampling different types of aquatic habitats (Table 1). This strategy was necessary, however, to assess the CS of a region at partitioning the entire diversity of the fauna.

Ecological Regions and Watersheds. Ecological regions had higher CS than did watershed basins on a similar scale (Figs. 3–5). Ecological regions include a variety of physical and biological data such as climate, vegetative cover, and geology. These variables could potentially affect caddisfly distributions. In contrast, watershed basins are simply hydrologic units and do not incorporate ecological data. This phenomenon was noted by Hawkins et al. (2000) who found that watersheds had a higher CS than ecological regions only when they were smaller than the corresponding ecological regions (see "Spatial Effects").

Previous studies using aquatic organismal data have found that the highest CSs (>10) of ecological regions occurred in areas with notable topographic and climatic variation, such as the South Platte River Basin (Tate and Heiny 1995), Ozark Highlands and Plains (Rabeni and Doisy 2000), Australian Highlands and Lowlands (Marchant et al. 2000), Alaska Range (Oswood et al. 2000), Rocky Mountains and Wyoming Basin, and the Victoria region of Australia (Newall and Wells 2000). Climate and topographic relief appeared to be more important to partitioning the variation of the aquatic biota than vegetative cover, geology, or the other common variables used in forming ecological regions. Many aquatic organisms can exist in only a limited temperature range; likewise, the change in the physical force of stream flow promoted by topographic variation is an important factor in determining aquatic organismal assemblages (e.g., Allan 1995).

In Minnesota, environmental temperature decreases in a northeasterly direction (Baker et al. 1985). Minimal topographic variation exists in Minnesota up to the eastern border where the Lower Saint Croix and Mississippi River gorges, as well as the Lake Superior Rift Zone promote relatively high relief (Borchert and Yaeger 1968). Level of disturbed habitat also decreases in an approximately northeasterly direction (USGS 1999). Houghton (2004) found that temperature, stream gradient, and level of disturbed habitat correlated with caddisfly species assemblages in Minnesota and thus were the most important factors in determining caddisfly regions. The Red River Valley ecological section likely had the highest CS among ecological sections because it encompassed an area of similar temperature, topography, and land use, thereby increasing W_i and overall CS (Figs. 3–5). The borders of this region were similar to those of the Northwestern caddisfly region and included almost identical sampling points (Figs. 1–2). The Minnesota and Iowa Morainal ecological section contained considerable temperature variation because of its large latitudinal range. It, therefore, had a W_i value lower than B and, thus, negative CS (Figs. 3–5).

A similar situation occurred with watershed basins. Among primary watersheds, the Saint Lawrence Seaway had by far the highest CS (Fig. 1). This region corresponded closely to the Lake Superior caddisfly region (Fig. 2). It was also the smallest of the three primary watersheds (see "Spatial Effects"). The Lake Superior, Red River Valley, and Saint Croix secondary watersheds all had consistently higher than average CS among secondary watersheds (Figs. 3–5). The Lake Superior and Red River Valley watersheds had borders similar to the Lake Superior and Northwestern caddisfly regions (Figs. 1–2) and encompassed areas of similar temperature, topography, and land use (Fig. 1). The same was true for the Saint Croix watershed, even though it was not by itself similar to a caddisfly region (Fig. 3.1). The Mississippi River watershed likely had the lowest W_i and CS due to variations in temperature and land use (Fig. 1).

Spatial Effects. Secondary groupings of ecological region and watershed basins had a higher CS than did primary groupings (Figs. 3–5) confirming the results of several previous studies (see Hawkins et al. 2000). Likewise, the smaller average unit size of caddisfly regions compared to biotic province and primary watershed may have contributed to its higher CS relative to these other regimes. The higher CS of smaller regions may have been due to several factors.

Smaller regions have less environmental heterogeneity relative to that which occurs between the regions. Ecological regions and watersheds that encompassed areas of similar temperature, stream gradient, and land use had higher CS than those that encompassed areas with a range of these values. Regardless of the exact placement of a region, however, smaller units are likely to have less environmental variation simply because they are smaller (e.g., Hawkins et al. 2000) and this will increase the value of W_i.

Smaller regions may also have had a higher CS because sampling sites were more contiguous. Van Sickle and Hughes (2000) found that geographic clusters had a higher CS than did any *a priori* classification. McCormick et al. (2000) determined that similarity between sites decreased as a function of the distance between sites. Smaller regions will have, on average, less distance between sampling sites than will large regions. This close proximity of sites will likely decrease the value of B and increase CS in small regions even if the sites are grouped without consideration of environmental variables. This may be particularly true with watershed basins. Although differences in physical variables that determine aquatic organismal distributions such as stream gradient, water chemistry, or substrate may exist between watersheds, such regions are essentially geographic, not biological partitions (Hawkins et al. 2000).

Taxonomic Resolution. CS increased with increased taxonomic resolution for all classifications (Figs. 3–5). For all classifications, both B and W decreased with increased taxonomic resolution; there was less chance of any two sites having a lower taxon in common than a higher taxon. W exhibited a smaller decrease than B with increasing resolution; a lower taxon was more likely to be unique to a region than a higher taxon. The majority of CS studies to date have found that increasing taxonomic resolution increases CS of the sampling grouping with both vertebrates (Van Sickle and Hughes 2000) and invertebrates (Marchant et al. 2000, Hawkins and Norris 2000, Hawkins and Vinson 2000, Feminella 2000, Hawkins et al. 2000, Waite et al. 2000). Identification to the lowest taxon possible has the greatest ability to discern biological differences among sites, thereby increasing the power of biological water quality monitoring, particularly subtle changes in water quality (Resh and Unzicker 1975, Cranston 1990, Resh and McElravy 1993). Some workers argue, however, that this increase in CS is of minimal importance compared to the added difficulty and expense of species-level identification, and that general trends in family data parallel those of species data, especially in the case of more drastic environmental changes (Warwick 1993, Bowman and Bailey 1997, Feminella 2000). For many aquatic invertebrates, including caddisflies, species-level identification is not possible with larvae, necessitating the use of families or genera regardless of their relative merits.

In their review of CS literature, Hawkins et al. (2000) found a typical decrease in CS of 0.03–0.10 (ca. 10–25%) when decreasing taxonomic resolution from genus-species to family. Those results are consistent with the current study. It is difficult to judge the biological significance of this documented decrease. While probably important, the 20% decrease in CS with decreasing taxonomic resolution found here is certainly less than the ≈ 50% decrease in CS *a priori* classifications. Hawkins et al. (2000) likewise found that classification method was more important than level of taxonomic resolution.

Implications for Biomonitoring. It was not surprising that caddisfly region—theoretically the optimal partitioning of the fauna—had a substantially higher CS than did *a priori* geographic classifications. The magnitude of the difference—approximately double— leads to some potentially troubling implications for monitoring the aquatic biota. Geographic classifications, such as watershed and ecological region, are widely used as sampling units and will likely remain so in the future. The results of this study suggest that such units are not the most appropriate for sampling caddisflies. For example, the Deciduous Forest biotic province encompasses considerable portions of the Northern,

Southern, and Southeastern caddisfly regions, each of which contains a disparate caddisfly fauna (Figs. 1 and 2) (Houghton 2004). Comparing aquatic habitats of the Deciduous Forest without considering this disparity would likely yield spurious information about human disturbance due to the natural faunal differences. This phenomenon is likely not limited to caddisflies; further research is needed to test the congruence of other aquatic organismal distributions with geographic classifications and with each other. If the distributions of aquatic organisms all exhibit a similar pattern, it may be valuable to replace the currently used geographic regions with organismal regions.

ACKNOWLEDGMENTS

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